THE MICROMORPH ALBIAN AMMONITE *FALLOTICERAS* PARONA AND BONARELLI

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ABSTRACT. *Falloticeras* Parona and Bonarelli, 1897 (type species: *Ammonites proteus* d'Orbigny, 1842) is a diminutive Cretaceous (Middle Albian, *dentatus* Zone) member of the acanthoceratacean subfamily Mojsisovicsiinae, individuals of which are generally adult at less than 35 mm diameter. The genus is considered to be a micromorph, perhaps a neotenous offshoot of *Mojsisovicsia* Steinmann, 1881, rather than simply a microconch of that genus. This is suggested by differences in ontogenetic development, relative abundance, and stratigraphic distribution. The type specimens are illustrated photographically for the first time, a lectotype designated, and the range of variation discussed.

THE genus *Falloticeras* Parona and Bonarelli (Acanthocerataceae) is a rare dwarf ammonite known originally from condensed sediments in the Alpes Maritimes, France, and subsequently recorded from the *spathi* subzone of the *dentatus* Zone in the Anglo-Paris Basin; both of which lie in the area of the hoplitinid or European faunal province. Besides redescribing and analysing populations from France, we record for the first time the presence of this genus in strata of equivalent ages in Zululand and Peru, areas well outside the hoplitinid province. Its rarity is not, therefore, due to faunal provincialism. The present study indicates that *Falloticeras* is best considered a neotenous offshoot, adult at 25–35 mm diameter, of *Mojsisovicsia* Steinmann, 1881, which is adult (in the type species at least) at diameters in excess of 100 mm, rather than a sexual dimorph.

D'Orbigny's type material is redescribed and figured for the first time, together with abundant topotype material, in an attempt to illustrate the range of variation within this monospecific genus.

SYSTEMATIC DESCRIPTION

Suborder AMMONITINA Hyatt, 1889
Superfamily ACANTHOCERATACEAE Hyatt, 1900
Family BRANCOCERATIDAE Spath, 1933
Subfamily MOJSISOVICSIINAE Hyatt, 1903
Genus FALLOTICERAS Parona and Bonarelli, 1897

Type species. Ammonites proteus d'Orbigny, 1842, p. 624, by the original designation of Parona and Bonarelli 1897, p. 89.

Diagnosis. Shell small, moderately involute, with a subquadrate, generally depressed whorl section. Early whorls with simple, broad, prorsiradiate ribs, projected on the venter to meet a fine siphonal keel at an acute angle. Ornament declines in maturity and the last half of the body chamber is commonly smooth. Constrictions variably developed. Sutures simple, with rather broad, slightly divided elements.

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Measurements. D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilical diameter. All measurements are in millimetres; figures in parentheses are dimensions as a percentage of total diameter.

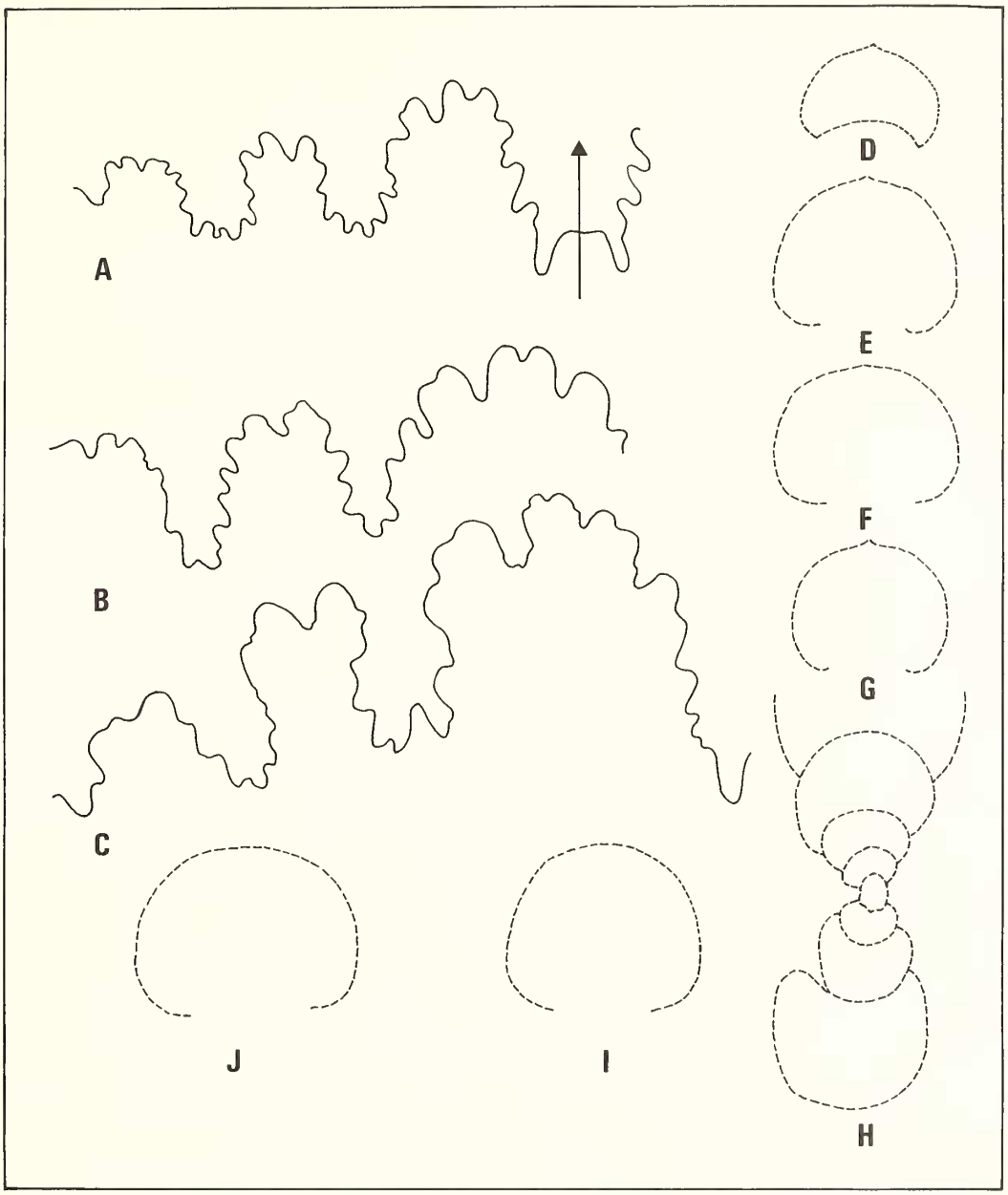
	D	Wb	Wh	Wb/Wh	U
*BMNH C68140	29	9(31)	8·5(29)	1·06	9(31)
BMNH C68140	21	7(33)	8(38)	0·88	7(33)
BMNH C68140	14·5	6(41)	6(41)	1·00	5(34)
BMNH C68145	25	9(36)	12(48)	0·75	10(40)
BMNH C68145	22	7(32)	11(50)	0·64	6·5(30)
MNHP 5766a	25	9(36)	*c.* 12(48)	0·75	*c.* 9(36)
MNHP 5766d	*c.* 24	8(33)	9(38)	0·89	*c.* 8(33)
BMNH C68141	22	7(32)	12·5(57)	0·56	8·5(39)
BMNH C68141	18·5	6(32)	11(59)	0·56	6·5(35)
MNHP 5766c	22	8(36)	10(45)	0·80	7(32)
BMNH C68142	20·5	7(34)	9(44)	0·78	7·5(37)
BMNH C68142	15·5	5(32)	8(52)	0·63	5(32)
BMNH C68146	20	9(45)	10(50)	0·90	7(35)
BMNH C68146	14	4·5(32)	*c.* 8(57)	0·56	*c.* 4·5 (32)
BMNH C68143	20	7(35)	11(55)	0·64	7(35)
BMNH C68143	15	5(33)	8(53)	0·63	5·5(37)
MNHP 5766b	19	7(37)	8(42)	0·88	7(37)
MNHP 5766b	15	5(33)	7(47)	0·71	5(33)
MNHP 5766e	*c.* 18	7(39)	10(56)	0·70	—
BMNH C2298	17	6·5(38)	8(47)	0·81	6(35)
MNHP 5766f	14	5·5(39)	6·5(46)	0·85	4(29)
BMNH C68144	10	3(30)	6(60)	0·50	3·5(35)
BMNH C68144	*c.* 7·5	2·5(33)	5(66)	0·50	2(27)

BMNH: British Museum (Natural History) Collections. MNHP: d'Orbigny Collection, Museum d'Histoire Naturelle, Paris. *c.*: approximately.

*Lectotype.

Discussion. Only the type species, *F. proteus*, has been referred to *Falloticeras*. The distinctive features are the small size, ribbed early but smooth adult whorls, constrictions, and delicate but distinct keel, which is commonly lost on the body chamber. All other members of the Mojsisovicsiinae reach much larger sizes than *Falloticeras*. *Mojsisovicsia* are mature at diameters up to 100 mm (e.g. BMNH C78865); *Oxytropidoceras* and its subgenera are commonly adult at between 100 and 300 mm (Spath 1921; Collignon *in* Besairie 1936); *Diploceras* are adult at 50–200 mm (e.g. Van Hoepen 1941). However, juvenile *Mojsisovicsia* show remarkable similarities to *adult Falloticeras* (see Pl. 105, figs. 1*a–c*, 4*a–b*, 12*a–b*, 13). They are smooth or faintly ribbed, and bear a distinct keel as does *Falloticeras*; contemporary species differ in showing a lack of strong ribbing on the earliest whorls (Pl. 105, figs. 4*a–b*, 13) and developing, abruptly, the very strong adult ornament of strong ribs, flares, umbilical and ventrolateral tubercles (Pl. 105, figs. 2*a–c*, 13; text-fig. 2). Medium-sized and adult individuals (e.g. Pl. 105, fig. 18) are unmistakably different.

Oxytropidoceras and its subgenera are usually oxycone, and may be strongly ribbed, tuberculate, or sometimes virtually smooth. We figure here two juveniles which show the smooth early stages (Pl. 105, figs. 8*a–c*, 9*a–c*; text-fig. 2) as in *Mojsisovicsia*, and the change to ribbing characteristic of middle and later growth. Here again, the ontogenetic changes in ornament are the *reverse* of those seen in *Falloticeras*. *Dipoloceras* is equally distinctive (Pl. 105, figs. 16, 17*a–c*, 18, 19*a–b*;



TEXT-FIG. 1. Sutures and whorl sections of *Falloticeras proteus* (d'Orbigny). A, JC 811–705C; B, the lectotype, BMNH C68140; C, BMNH C2298. All ×12·5. D, MNHP 7566c; E, MCd; F, BMNH C6814; G, MCc; H, MCe; I, MCa; J, MCb. All ×4 except H, which is ×6.

text-fig. 2). Evenly ribbed forms such as *Dipoloceras bouchardianum* (d'Orbigny) virtually lack ribs up to diameters of 3–4 mm (Pl. 105, fig. 17*b*; text-fig. 2); beyond this, strong ribs are developed throughout ontogeny. In more typical members of the group, such as *D.* cf. *pseudaon* Spath (Pl. 105, figs. 16, 19*a–b*) very strong, coarse ribbing also succeeds an initial smooth stage, here augmented by ribs which flare at the point of branching and are decorated by spiral, *Elobiceras*-like crenulations (Pl. 105, fig. 19*a*). In all *Dipoloceras*, the keel is much stronger than in *Falloticeras*, and retained throughout ontogeny.

Members of the Brancoceratinae such as *Eubrancoceras* Breistroffer, 1952, *Brancoceras* Steinmann, 1881, and *Hysteroceras* Hyatt, 1900, all lack the delicate keel and are strongly ribbed capricorns in middle and late growth stages. The morphologically closest member of this group is the subgenus *Eubrancoceras* (*Parabrancoceras*) Breistroffer, 1952, which has constrictions on the inner whorls; the outer whorls are, however, distinctively capricorn.

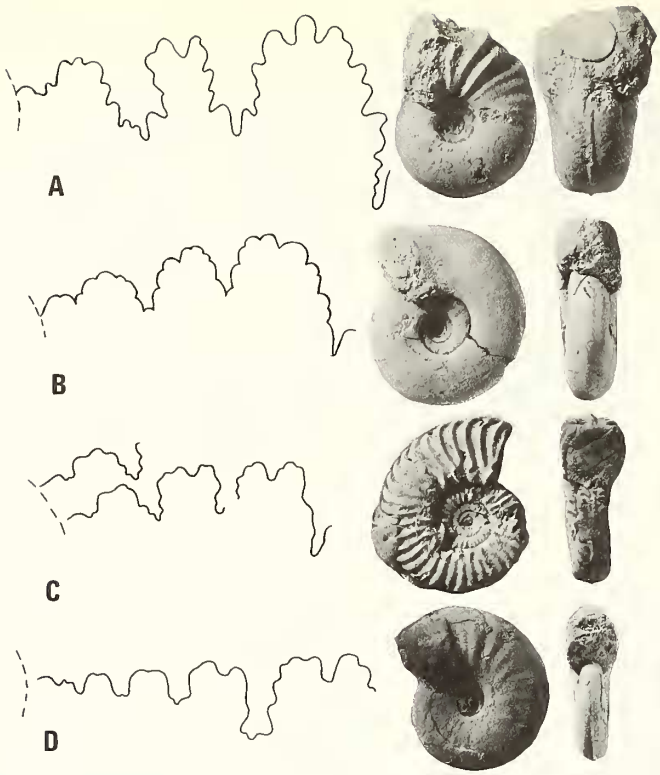
Occurrence. D'Orbigny's remaining specimens of *Falloticeras* are simply labelled 'Clar' (Alpes Maritimes). From the phosphatic preservation and sandy glauconitic matrix they clearly derive from one of the phosphatic sequences known in the Albian of this area, resembling closely the preservation of material from Escragnolles (Alpes Maritimes) before us. The species has been recorded independently from Escragnolles by Parona and Bonarelli (1897), Breistroffer (1947), and Collignon (1949) amongst others, and from Gourdon (Alpes Maritimes) by Collignon (1949). Both of these sequences are highly condensed, and the *Falloticeras* cannot be precisely placed zonally in this region. In terms of English zonal and subzonal sequence proposed by Casey (1961) and Owen (1971), the faunas from Escragnolles (Collignon 1949) suggest horizons from the lowest Albian *Leymeriella tardefurcata* Zone to the *Dipoloceras cristatum* Zone of early late Albian age. At Gourdon, a broadly similar ammonite fauna occurs, and General M. Collignon tells us that it is his view that the *Falloticeras* are confined to the Middle Albian *Hoplites dentatus* Zone.

Falloticeras has also been recorded from one horizon and locality in England, the *spathi* subzone of the *dentatus* Zone of the Gault Clay at Wrotham, Kent (Casey 1959; Milbourne 1963; Owen 1971). To these European occurrences, we can now add records from South America and South Africa. The first of these is based on a re-examination of the material from the Middle Albian of Saco near Oroya, Peru, described by Douglas (1921). Amongst previously unfigured material is what may be an undescribed *Falloticeras* species (OUM KU 81; Pl. 105, fig. 14*a–b*).

EXPLANATION OF PLATE 104

Figs. 1*a–c*–19*a–c*. *Falloticeras proteus* (d'Orbigny). All specimens are phosphatic internal moulds, retaining traces of test. 1*a–c*–6*a–c*, 18*a–c*–19*a–c* are specimens in the d'Orbigny Collection, Muséum d'Histoire Naturelle, Paris, and are from the Middle Albian of Clar, near Escragnolles, Alpes Maritimes, France. 1*a–c* are MNHP 5766g; 2*a–c* are MNHP 5766a; 3*a–b* are MNHP 5766b; 4*a–b* are MNHP 5766e; 5*a–c*, 19*a–c* are MNHP 5766f; 6*a–e*, 18*a–c* are MNHP 5766c; 7*a–b*–17*a–b* are a variation series from the Middle Albian of Gourdon, Alpes Maritimes, France (M. Collignon Collection); 18*a–c*–19*a–c* are figured × 2, all the rest × 1.

KENNEDY and COOPER, *Falloticeras* from the Albian of France



TEXT-FIG. 2. Comparative developmental stages of A, *Mojsisovicsia* sp. juv., BMNH C68147, Middle Albian, Escragnolles; B, *Falloticeras proteus* (d'Orbigny), the lectotype BMNH C68140, Middle Albian, Escragnolles; C, *Dipoloceras bouchardianum* (d'Orbigny), BMNH C79611, *cristatum* Subzone, Wrotham, Kent; D, *Oxytropidoceras* sp. juv. BMNH 78785a; Albian 'South of France'. All specimens are ×2; sutures ×12·5.

EXPLANATION OF PLATE 105

Fig. 1*a–c*. *Mojsisovicsia* sp. juv. BMNH C68147, Middle Albian, Escragnolles, Alpes Maritimes (Astier Collection).

Figs. 2*a–b*, 5*a–c*, 7*a–b*. *Falloticeras* aff. *proteus* (d'Orbigny). BMNH C68145, C68143, and C68146. Middle Albian, Escragnolles, Alpes Maritimes (Astier Collection).

Figs. 3*a–c*, 6*a–b*. *Falloticeras proteus* (d'Orbigny). 3*a–c* the lectotype, BMNH C68140, 6*a–b* a paralectotype, BMNH C68142, both in the Astier Collection, Middle Albian, Escragnolles, Alpes Maritimes.

Figs. 4*a–b*, 12*a–b*. *Mojsisovicsia* sp. juv. BMNH C78872 and C78865. Middle Albian, Mzinene Formation, Mzinene River, Zululand (South Africa).

Figs. 8*a–c*, 9*a–c*. *Oxytropidoceras* sp. juv. BMNH 78783a-b, 'South of France' (Astier Collection).

Fig. 10*a–b*. *Falloticeras* sp. BMNH C78873 and C78871, from the Middle Albian, Mzinene Formation, Mzinene River, Zululand (South Africa).

Figs. 11, 13, 18. *Mojsisovicsia ventanillensis* (Gabb). OUM KU 88, 84, and 80, Middle Albian of Saco, near Oroya, Peru (J. A. Douglas Collection).

Fig. 14*a–b*. *Falloticeras* sp. OUM KU 81, Middle Albian of Saco, near Oroya, Peru (J. A. Douglas Collection).

Figs. 16, 19*a–b*. *Dipoloceras* cf. *pseudaon* (Spath). Van Hoepen Collection, South African Museum, Cape Town (figured ×2) and BMNH C78882. Upper Albian, Mzinene Formation, Mzinene River, Zululand (South Africa).

Fig. 17*a–c*. *Dipoloceras bouchardianum* (d'Orbigny). BMNH C79611, Upper Albian, Lower-Upper Gault Junction Bed, Division 6, ex *cristatum* subzone. Rugby Portland Cement Co. Pit, 450 yards North of Ford Place House, Wrotham, Kent (H. G. Owen Collection). All figures ×1, unless otherwise stated.

KENNEDY and COOPER, Albian ammonites

The second new record is from the Middle Albian of Zululand, South Africa, where collections from the lower part of the Mzinene Formation on the Mzinene (Umsinene of authors) River near Hluhluwe (Locality 51, bed 1 of Kennedy and Klinger 1975) have yielded a further series of *Falloticeras* (BMNH C78868, 78870–78871, 78873; Pl. 105, figs. 10*a–b*, 15*a–b*). The Zululand material occurs associated with *Mojsisovicsia* aff. *ventanillensis* (Gabb), *Phylloceras* (*Hypophylloceras*) *velledae velledae* (Michelin), *Oxytropidoceras* (*Manuaniceras*) *manuanense* (Spath), *Pseudhelicoceras catenatum* (d'Orbigny), and *Puzosia* sp. juv., again suggesting a Middle Albian age.

Falloticeras proteus (d'Orbigny)

Plate 104; Plate 105, figs. 2, 3, 6, 7, 10, 15; text-figs. 1–3

1842 *Ammonites proteus* d'Orbigny, p. 624.
1850 *Ammonites proteus* d'Orbigny; d'Orbigny, p. 124.
1860 *Ammonites proteus* d'Orbigny; Pictet and Campiche, p. 306.
1897 *Falloticeras proteum* (d'Orbigny); Parona and Bonarelli, p. 89, pl. 12, fig. 1.
1922 *Falloticeras* . . .; Spath, p. 97.
1931 *Falloticeras* . . .; Spath, pp. 346, 352.
1938 *Falloticeras proteum* (d'Orbigny); Roman, p. 370, pl. 37, fig. 353*a–b*. (Copy of Parona and Bonarelli 1897.)
1942 *Falloticeras* . . .; Spath, p. 708.
1947 *Falloticeras proteus* d'Orbigny; Breistroffer, p. 30.
1949 *Falloticeras proteus* d'Orbigny; Collignon, p. 122.
1957 *Falloticeras proteus* (d'Orbigny); Wright *in* Arkell *et al.*, p. L404.
1959 *Falloticeras* cf. *proteus* (d'Orbigny); Casey, p. 207.
1963 *Falloticeras proteus* (d'Orbigny); Milbourne, Table 1.
1971 *Falloticeras proteum* (d'Orbigny); Owen, p. 155.

Type material. D'Orbigny introduced the name *proteus* in 1842, stating that the species had been discovered by Astier in the 'gault supérieur' of Clar, near Escragnolles. D'Orbigny's collection (which was catalogued in 1858–1860, after his death in 1857) contains six specimens of *Falloticeras* under the catalogue number 5766. Associated with them is a label, apparently in d'Orbigny's hand, as follows:

Clar
Gault
am. Proteus avec intérieur
(Mouton)

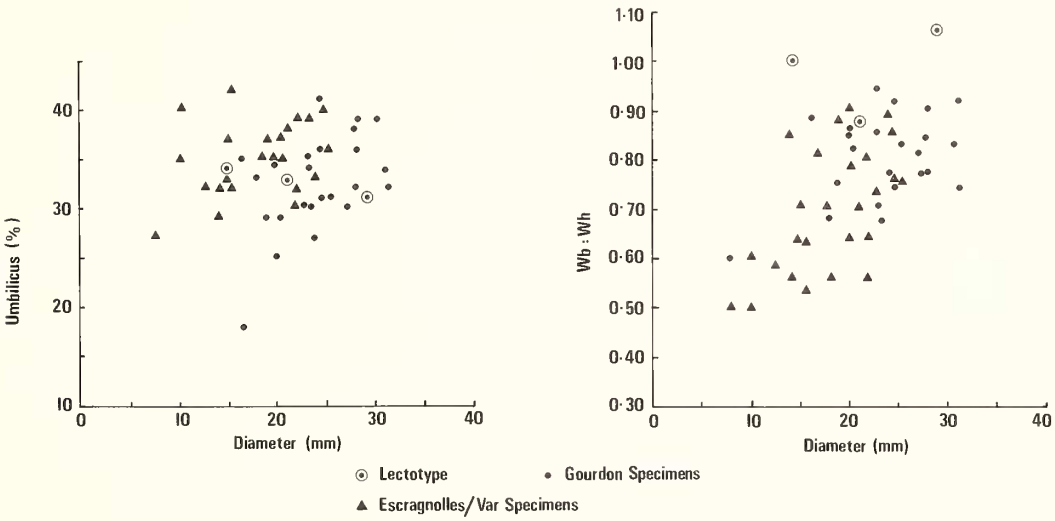
D'Orbigny's collection contains many specimens in addition to those cited in his publications, including in some cases more than one specimen of species originally described on the basis of single specimens, and also specimens of manuscript species, whilst in other instances d'Orbigny returned specimens to other workers after describing and naming them. Astier's collection was purchased (in 1853) by, and is now housed in, the British Museum (Natural History), and there are seven specimens which could be regarded as *Falloticeras*, BMNH C68140–68142, C681404–681406, and C2298. The d'Orbigny and Astier specimens all occur in a similar preservation. While it is, in our view, quite impossible to be certain whether all or any of these specimens were studies by d'Orbigny prior to publication of the name *proteus* in 1842, it is reasonable to regard the specimens in the Astier Collection as part of the syntype series, and we designate one of these, BMNH C68140 (Pl. 105, fig. 3*a–c*; text-fig. 2*b*) as lectotype.

Other specimens studied. Three topotypes, 811-705*a–c* in the Jaubert Collection, housed at the Université Paris VI, also from Clar (Alpes Maritimes). Twenty-one specimens from the condensed Albian sequence of Gourdon (Alpes Maritimes), kindly loaned by General M. Collignon (MCa–k).

Diagnosis. As for genus; see above.

Description. All specimens are phosphatic internal moulds; a few retain traces of phosphatized shell.

Up to 15 mm diameter. Shell strongly inflated, involute, almost cadicone, the whorl breadth to height ratio varying between 0·5 and 0·85 (text-figs. 1, 3). Whorls reniform to subelliptical in cross-section, greatest breadth low on the flank. Umbilicus generally narrow, conical, with steeply inclined walls and an evenly rounded shoulder. Flanks strongly rounded, venter somewhat flattened with a narrow, delicate, continuous siphonal keel (Pl. 104, fig. 6*a*, *c*; Pl. 105, fig. 6*a–b*). Low, broad, simple ribs arise at the umbilical seam as mere striations, to strengthen across the umbilical shoulder and flank. They are commonly broader than the interspaces, rounded, concave, and markedly prorsiradiate (Pl. 104, figs. 3*b*, 6*b*, 18*c*), being projected forwards across the ventrolateral shoulder and venter to meet the siphonal keel at an acute angle. There are between twenty-four and thirty ribs per whorl in the material before us. Weak to strong constrictions, parallel to the ribs, are present in some specimens (e.g. Pl. 104, figs. 4*a*, 5*a–b*, 19*a–c*).



TEXT-FIG. 3. Graphical analysis of variation in *Falloticeras proteus* (d'Orbigny).

15–32 mm diameter. The shell becomes progressively more evolute (umbilicus up to 44% of diameter), degree of evolution increasing with size, the body chamber itself tending to uncoil in some individuals (e.g. Pl. 104, figs. 7*b*, 8*b*, 13*a*, 16*b*; Pl. 105, figs. 3*b*, 6*b*) giving a scaphitoid coiling. The umbilicus becomes shallower, flanks flatten, the ventrolateral shoulder approaches the subangular, and the venter flattens (Pl. 104, figs. 10*b*, 14*a*) or tends to slight concavity. Ribbing generally declines, and disappears progressively between diameters of 7 and 15 mm. The siphonal keel persists on to the outer whorl (e.g. Pl. 104, figs. 2*a*, 6*c*, 15*a*) but generally declines on the later parts of the body chamber (Pl. 104, figs. 1*c*, 8*a*, 11*b*; Pl. 105, fig. 3*a*). The aperture of mature forms is preceded by a broad, shallow constriction (Pl. 104, figs. 1*b*, 9*a*, 13*a*; Pl. 105, fig. 3*b*), succeeded by a distinct flare (e.g. Pl. 104, fig. 9*a*; Pl. 105, fig. 3*b*). The aperture is gently sinuous in lateral view, with a distinct ventral peak (Pl. 104, fig. 15*b*).

Sutures (text-figs. 1, 2). The sutures of mature *Falloticeras* are very simple, with broad, little incised elements.

Intraspecific variation. Juveniles show a wide variation in strength of ribbing (compare Pl. 104, figs. 3*b*, 6*b*, 18*c*, with Pl. 104, figs. 5*a–c*; 19*a–c*; Pl. 105, fig. 15*a–b*) from near obsolete to strong. In most individuals, the strength of ornament declines between 7 and 15 mm, thereafter disappearing. A few specimens, e.g. MCf (Pl. 104, fig. 11*a*), retain their ribs to over 20 mm. Constrictions are very variably developed; they are commonly absent in ribbed juveniles (Pl. 104, figs. 6*a–c*, 18*a–c*) but may be conspicuous on feebly ornamented ones (Pl. 104, figs. 5*a–c*, 19*a–c*), a few specimens tentatively referred to this species retaining both

characteristics (Pl. 105, figs. 2*a–b*, 7*a–b*). The keel is very variably developed; in some (Collignon's 1949 var. nov.) it is retained to the mature aperture (Pl. 104, fig. 15*a–c*), but in most it disappears. Exceptionally faint but distinctive spiral strigations are developed (Pl. 105, fig. 3*a–c*).

Over-all relative proportions vary greatly, as is clear from the table of dimensions, plots in text-fig. 3 and the variation series figured on Plate 104, with a continuum from robust specimens (Pl. 104, fig. 7*a–b*) to slender (Pl. 104, fig. 11*a–b*), and flat-sided (Pl. 104, fig. 10*a–b*) to round-whorled (Pl. 104, fig. 16*a–b*) individuals. The whorl breadth–height ratio changes from relatively depressed to compressed throughout ontogeny; the variation in whorl breadth–height ratio being as follows (diameter and Wb:Wh) 14 mm, 0·53–1·00: 20 mm, 0·56–0·98: 30 mm, 0·74–0·92. There is also a tendency towards more evolute coiling as size increases, but again there is a range (diameter, umbilical width): 17 mm, 19–41%: 25 mm, 28–41%: 30 mm, 31–39%. There are a few specimens in the British Museum (Natural History) (Astier Collection), which we are unable to place in *F. proteus* with complete confidence; they include BMNH C68145 and C68146; both are far more strongly constricted than typical forms (Pl. 105, figs. 2*a–b*, 7*a–b*) and have strong ribs associated with the constrictions which may develop umbilical bullae (Pl. 105, fig. 2*b*). Both bear a delicate *Falloticeras*-like keel, and for the present we would identify them as *F.* aff. *proteus*; they may indicate, however, the presence of a second species at Escragnolles.

Occurrence. As for genus (see above).

Discussion. The only forms liable to be confused with *F. proteus* belong to other genera, and these are discussed above under the account of the genus. Text-fig. 2 compares juveniles of all genera of Mojsisovicsinae; the closest form morphologically is *Mojsisovicsia* itself, most species of which can be distinguished by lack of ornament on early whorls, a stronger keel, and sudden acquisition of strong ribbing after a smooth or feebly ornamented stage as size increases, rather than the progressive loss of ornament seen in *Falloticeras*.

A certain amount of confusion appears to surround the date of introduction of the name *proteus*; it is first used on p. 624 of *Paléontologie Française*, *Terrains Crétacés Céphalopodes*, in a list of the cephalopods of the 'gault supérieur', and diagnosed in a footnote as follows: 'Cette Ammonite vient de Clar, près d'Escragnolle (Var.). Elle y a été découverte par M. Astier. Elle est remarquable en ce qu'elle n'a des côtes, qu'etant jeune; plus tard, elle est entièrement lisse et porvue d'une carène, comme les *A. varicosus* et *Delaruei*.' This is a perfectly acceptable indication, and the species thus dates from 1842, rather than 1840 or 1850 as indicated by some authors. The species is named for the sea god Proteus of classical mythology (although as Ovid (*Metamorphoses*) observes, the latter showed rather more extreme changes in morphology than the ammonite bearing his name, having appeared as a young man, a lion, a raging wild bear, snake, bull, stone, and tree, as running water, a river, and fire on occasion). The name should therefore be spelt *proteus*; *proteum* is an error.

DISCUSSION

Our description and illustrations of *F. proteus* demonstrate how very different adults are from all other *adult* members of the Mojsisovicsinae, although they are similar in many respects to juveniles of associated *Mojsisovicsia* (e.g. compare Pl. 105, figs. 1 and 3; Pl. 105, figs. 4, 10, and 12; Pl. 105, figs. 13 and 14). Since the two occur together at all known localities of *Falloticeras*, one must consider whether the genus is not only a micromorph, but also a microconch, that is to say the male of *Mojsisovicsia*.

The following observations run counter to this suggestion: 1, in *Falloticeras*, the early whorls are generally ribbed (e.g. Pl. 105, figs. 6*b*, 15*a*). In *Mojsisovicsia* the

reverse is generally the case (Pl. 105, figs. 1*b*, 4*b*, 12*a*, 13). 2, in *Falloticeras* the keel declines at maturity, in *Mojsisovicsia* it strengthens. 3, although *Falloticeras* always occurs with *Mojsisovicsia*, the latter has a somewhat wider geographic distribution. 4, *Falloticeras* is always much rarer than *Mojsisovicsia*, whereas only one species of *Falloticeras* occurs in the type area, there are several *Mojsisovicsia* species recorded. 5, the recorded stratigraphical range of the two genera are different. *Falloticeras* is confined to the *Hoplites dentatus* Zone of the Middle Albian (*spathi* subzone in England), and its equivalents, whilst *Mojsisovicsia* ranges as high as the *Euhoplites loricatus* Zone (*delaruei* subzone in England).

Thus there is a strong case for regarding *Falloticeras* as a micromorph genus. A comparison of juveniles of the other genera of the subfamily (text-fig. 2) suggests that the genus arose as a result of neoteny, with *Mojsisovicsia* as a possible ancestor. If *Falloticeras* is a neotenous micromorph, the evolutionary experiment appears to have been less than successful, for *Falloticeras* was, as far as we know, an evolutionary cul-de-sac. It is not in the mainstream of brancoceratid evolution, and it lacks descendants, as do several other micromorph Acanthocerataceae such as the Flickiidae, and the acanthoceratinid *Neosaynoceras*. However, this type of evolution can lead to evolutionary success, with neotenous micromorphs giving rise to new genera and subfamilies, for example, in the genus *Protacanthoceras* Spath, 1923 (Acanthocerataceae), the evolution of which is to be discussed by Wright and Kennedy elsewhere.

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REFERENCES

ARKELL, W. J. *et al.* 1957. *Treatise on Invertebrate Palaeontology* L., *Mollusca* (4). Univ. Kansas Press and Geol. Soc. Amer., xxii+L1–L490. Lawrence, Kansas and New York.

BESAIRIE, H. 1936. Recherches géologiques à Madagascar. Première suite. La géologie du nord-ouest. *Mém. Acad. Malagache*, **21**, 9–259, pls. 1–24.

BREISTROFFER, M. 1947. Sur les zones d'ammonites dans l'Albien de France et d'Angleterre. *Trav. Lab. Géol. Univ. Grenoble*, **26**, 1–88 (17–104).

CALLOMON, J. H. 1963. Sexual dimorphism in Jurassic ammonites. *Trans. Leicester lit. phil. Soc.* **57**, 21–56.

CASEY, R. 1959. Field meeting at Wrotham and the Maidstone By-Pass. *Proc. geol. Ass.* **70**, 206–209.

—— 1961. The stratigraphical Palaeontology of the Lower Greensand. *Palaeontology*, **3**, 487–621, pls. 77–84.

COLLIGNON, M. 1949. Recherches sur les faunes albiennes de Madagascar 1. L'Albien d'Ambarimaninga. *Annls géol. Serv. Mines Madagascar*, **14**, 1–128, pls. 1–22.

DOUGLAS, J. A. 1921. Geological sections through the Andes of Peru and Bolivia: III From the Port of Callao to the River Perene. *Q. Jl geol. Soc. Lond.* **77**, 246–284, pls. 15–20.

KENNEDY, W. J. 1977. Ammonite Evolution. *In* HALLAM, A. (ed.). *Patterns of Evolution*. Elsevier, Amsterdam, London, and New York.

—— and COBBAN, W. A. 1976. Aspects of Ammonite Biology, Biogeography and Biostratigraphy. *Spec. Pap. Paleont.* **17**, 93 pp., 11 pls.

—— and KLINGER, H. C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. *Bull. Br. Mus. nat. Hist.* (Geol.), **25**, 263–315, 1 pl.

MAKOWSKI, H. 1962. Problems of sexual dimorphism in ammonites. *Palaeont. pol.* **12,** 1–92.

MILBOURNE, R. A. 1963. The Gault at Ford Place, Wrotham, Kent. *Proc. geol. Ass.* **74,** 55–79, pls. 4, 5.

ORBIGNY, A. D'. 1840–1842. *Paléontologie Française, Terrains Crétacés.* I. Céphalopodes. 1–120 (1840); 121–430 (1841); 431–662 (1842); 148 pls.

—— 1850. *Prodrome de Paléontologie Stratigraphique Universelle des Animaux Mollusques et Rayonnés II.* Paris, 427 pp.

OWEN, H. G. 1971. Middle Albian Stratigraphy in the Anglo-Paris Basin. *Bull. Br. Mus. nat. Hist.* (Geol.), Suppl. **8,** 164 pp., 3 pls.

PARONA, C. F. and BONARELLI, E. G. 1897. Fossili albiani d'Escragnolles, del Nizzardo e della Liguria occidentale. *Palaeontogr. Ital.* **2,** 53–112, pls. 10–14.

PICTET, F. J. and CAMPICHE, G. 1858–1864. *Matériaux pour la Paléontologie suisse. Description des fossiles du terrain crétacé des environs de Sainte-Croix.* Geneva, 1–380, pls. 1–53.

ROMAN, F. 1938. *Les Ammonites Jurassiques et Crétacés.* Paris, 554 pp., 53 pls.

SPATH, L. F. 1921. On Cretaceous Cephalopoda from Zululand. *Ann. S. Afr. Mus.* **12,** 217–321, pls. 19–26.

—— 1922. On Cretaceous Ammonoidea from Angola, collected by Prof. J. W. Gregory, D.Sc., F.R.S. *Trans. R. Soc. Edinb.* **53,** 91–160, pls. 1–4.

—— 1923–1943. A monograph of the Ammonoidea of the Gault. *Palaeontogr. Soc.* [*Monogr.*], 787 pp., 72 pls.

VAN HOEPEN, E. C. N. 1941. Die gekielde Ammoniete van die Suid-Afrikaanse Gault. 1. Diploceratidae, Cechenoceratidae en Drepanoceratidae. *Paleont. Navors. nas. Mus. Bloemfontein,* **1,** 55–90, figs. 1–55, pls. 8–19.

WESTERMANN, G. E. G. (ed.), 1969. *Sexual dimorphism in fossil metazoa and taxonomic implications.* Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, iv+251.

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